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Impedance Modulation and Feedback Corrections in Tracking Targets of Variable Size and Frequency

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Selen, Luc P. J., Jaap H. van Dieën, and Peter J. Beek. Impedance modulation and feedback corrections in tracking targets of variable size and frequency. *J Neurophysiol* 96: 2750–2759, 2006. First published August 9, 2006; doi:10.1152/jn.00552.2006. Humans are able to adjust the accuracy of their movements to the demands posed by the task at hand. The variability in task execution caused by the inherent noisiness of the neuromuscular system can be tuned to task demands by both feedforward (e.g., impedance modulation) and feedback mechanisms. In this experiment, we studied both mechanisms, using mechanical perturbations to estimate stiffness and damping as indices of impedance modulation and submovement scaling as an index of feedback driven corrections. Eight subjects tracked three differently sized targets (0.0135, 0.0270, and 0.0405 rad) moving at three different frequencies (0.20, 0.25, and 0.33 Hz). Movement variability decreased with both decreasing target size and movement frequency, whereas stiffness and damping increased with decreasing target size, independent of movement frequency. These results are consistent with the theory that mechanical impedance acts as a filter of noisy neuromuscular signals but challenge stochastic theories of motor control that do not account for impedance modulation and only partially for feedback control. Submovements during unperturbed cycles were quantified in terms of their gain, i.e., the slope between their duration and amplitude in the speed profile. Submovement gain decreased with decreasing movement frequency and increasing target size. The results were interpreted to imply that submovement gain is related to observed tracking errors and that those tracking errors are expressed in units of target size. We conclude that impedance and submovement gain modulation contribute additively to tracking accuracy.

INTRODUCTION

Many tasks in daily life, such as handwriting, drawing, and computer work, require accurate movements. Although movement accuracy is limited by noise in the human motor system, the redundancy of this system offers control strategies to accommodate the accuracy constraints imposed by the task. For example, during keyboarding, the size of the keys defines the required spatial accuracy, whereas the structure and control of the neuro-musculo-skeletal system provides and constrains solutions to achieve the required accuracy.

A constraint of the neuromuscular system that has received much interest in recent theories of motor control is the signal dependency of neuromuscular noise (Harris and Wolpert 1998; Todorov and Jordan 2002). The proposed solution to attain a required accuracy level is to construct an optimal control signal, including feedback in the model of Todorov and Jordan (2002), in the sense that endpoint variability over successive trials is minimized. Although this approach reproduces many

movement features, it fails to offer a means to control kinematic variability when confronted with different accuracy demands under strict velocity and/or duration constraints (Schaal and Schweighofer 2005). Furthermore, this approach yields smooth movements that do not possess the characteristic irregularities observed in goal-directed aiming (Dounskaia et al. 2005; Fishbach et al. 2005; Milner and Ijaz 1990) and tracking movements (Miall et al. 1993; Pasalar et al. 2005; Roitman et al. 2004).

What mechanism(s) might reduce kinematic variability caused by neuromuscular noise? Van Galen and Schomaker (1992) and Van Galen and De Jong (1995) hypothesized that mechanical impedance attenuates the effects of neuromuscular noise on movement kinematics. Although impedance has been shown to stabilize the musculo-skeletal system in response to external perturbations (Burdet et al. 2001; Franklin et al. 2003), its modulation to reduce the effects of internal destabilizing perturbations seems paradoxical. On the one hand, muscular activity forms the source of force variability, whereas on the other hand, it provides a means of suppressing its kinematic effects (Schaal and Schweighofer 2005; Selen et al. 2005). In any case, experimental studies of both single-joint (Osu et al. 2004) and multijoint goal-directed movements (Gribble et al. 2003; Laursen et al. 1998; Sandfeld and Jensen 2005; Van Galen and Van Huygevoort 2000; Van Gemmert and Van Galen 1997; Van Roon et al. 2005; Visser et al. 2004) have shown that muscular coactivation increases with increasing accuracy demands. The hypothesis of impedance modulation was further supported by modeling studies (Selen et al. 2005; Van Galen and De Jong 1995) predicting a decrease of movement variability with increasing coactivation, despite increasing neuromuscular noise. The experimental evidence for impedance modulation was presented only recently (Selen et al. 2006). We showed that the mechanical impedance of the elbow is modulated as a function of accuracy demands in time-constrained goal-directed movements. Although we observed an increase in impedance, especially in stiffness, with increased accuracy demands, subjects also tended to increase movement time both by decreasing peak velocity and by making submovements. Apparently, the tendency to prolong movement duration in response to increased accuracy demands, as reflected in Fitts' law (Fitts 1954), is hard to suppress. This resulted in large variability in the realization of the movements, which partially obscured the modulation of impedance in response to increases in accuracy demands.

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Do submovements contribute to movement accuracy? Although the presence of submovements has been attributed to the intermittency of neural control, in goal-directed movements, their scaling is supposed to represent corrective actions to accommodate the prevailing accuracy constraints (Dounskaia et al. 2005; Milner and Ijaz 1990). The optimized submovement model of Meyer et al. (1988) offers an influential explanation of speed-accuracy relations in goal-directed aiming. The model proposes that rapid aiming movements may involve submovements whose durations are optimized to cope with a noisy neuromotor system, resulting in more corrective submovements and longer movement times for stricter accuracy constraints. More recently, a similar model, including both visual and proprioceptive feedback, was proposed that allowed for overlapping, prediction-based, submovements (Burdet and Milner 1998). For target tracking, it is unknown whether submovements contribute to accuracy and if and how their characteristics change with target size. Extending the results from goal-directed movements, we expect more frequent and more subtle submovements with smaller targets. In tracking, however, the velocity is predefined and poses constraints on the submovements. Those constraints have been found to result in submovements with invariant duration and increasing amplitude with increasing movement velocities (Miall et al. 1986; Pasalar et al. 2005; Roitman et al. 2004).

The objective of this study was not only to further investigate impedance modulation in response to accuracy constraints but also to examine whether and how submovements are regulated to accommodate accuracy constraints during single-joint target tracking. This task was chosen because the prescription of target motion provides a means to constrain movement velocity and thus might help to avoid the aforementioned masking of impedance modulation caused by timing variability. Furthermore, target tracking allows for movement within the target area and thus study of the contribution of submovements to accuracy demands. We therefore conducted an experiment in which subjects were invited to track a target presented on a light emitting diode (LED) array. The experiment consisted of nine conditions (3 target sizes \times 3 tracking frequencies). Impedance, expressed as stiffness (K) and damping (B), was estimated by applying controlled mechanical perturbations to the elbow joint during tracking. Characteristics of submovements were studied in the unperturbed trials.

METHODS

Subjects

Eight subjects (3 men and 5 women) between 20 and 28 yr of age participated in the experiment. All subjects had normal or corrected to normal vision and reported no history of neuromuscular disorders. The local Ethics Committee approved the experiment before its conductance, and all subjects signed informed consent forms before their participation. The experiment lasted ~ 2 h including preparation time. During the experiment, subjects were allowed to rest as often and as long as they wished to avoid fatigue. The data of one subject were removed from the impedance analysis but not from the accuracy and submovement analyses. For this subject, perturbations were distributed randomly over the movement cycle because of a programming error.

Apparatus

Figure 1 depicts the experimental set-up. Subjects were seated on a chair in front of a semicircular array of LEDs. Their dominant forearm (the arm they used for writing), including hand palm and wrist, was cast (NobaCast, Noba Verbandmittel Danz) onto a lightweight T-wedged bar. The bar was mounted on the vertical shaft of a torque controlled motor (S-motor, elu93028, Fokker Control Systems), with the medial epicondyle aligned with the motor's axis of rotation and the palm of the hand facing downward.

The height of the chair was adjusted such that the upper arm and forearm were in the horizontal plane. The LED array, consisting of 447 LEDs, was placed 1.5 m in front of the wrist of the cast arm. The forearm pointed at the center of the LED array when the elbow was flexed by 90° . A small laser pointer was attached to the lightweight bar indicating the pointing direction on the LED array. Two LEDs were illuminated, defining the boundaries of the to-be-tracked target.

The torque-controlled motor operated in closed loop fashion at 5 kHz. In the unperturbed cycles, the set-point of the controller was 0 Nm, resulting in a smooth and frictionless movement environment. The angular position of the motor shaft was measured by a potenti-

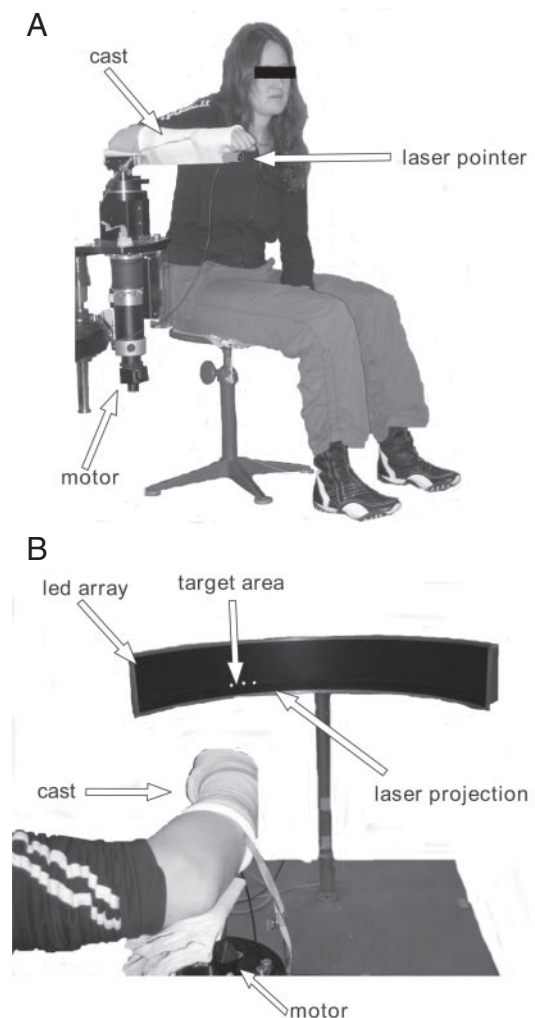


FIG. 1. Experimental set-up of target tracking experiment. *Top*: front-side view of a subject with the subject's forearm cast onto a lightweight bar attached to the motor. *Bottom*: LED array with target to be tracked and laser projection.

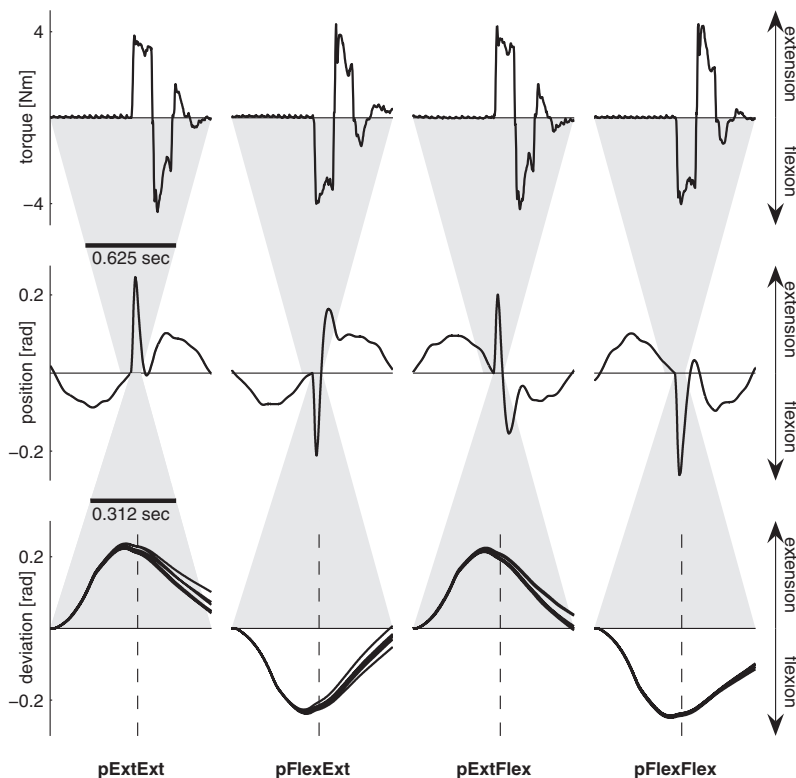


FIG. 2. Examples of effects of 4 perturbation types. In the 2 left panels, the subject was extending his elbow, while perturbations started in extension (pExtExt) and flexion (pFlexExt) directions, respectively. In the 2 right panels, the subject was flexing his elbow, while perturbations started in extension (pExtFlex) and flexion (pFlexFlex) directions, respectively. *Middle row*: full cycles (5 s) of elbow angle including a perturbation. *Top row*: part of motor torque (−312.5 to 312.5 ms of perturbation onset). *Bottom row*: kinematic effects of 6 perturbations after subtraction of target sine. Vertical line indicates end of impedance estimation time window (i.e., 0–170 ms). Gray areas indicate difference in times scales between panels.

ometer (22HSPP-10, Sakae), and the remaining torque was measured by a strain gauge. Both position and torque data were stored at 1 kHz.

Experimental task

Subjects were instructed to track a target whose boundaries were indicated by two LEDs. The target oscillated sinusoidally with amplitude (peak-peak) of 0.2 rad. Three differently sized targets (0.0135, 0.0270, and 0.0405 rad) were tracked at three movement frequencies (0.33, 0.25, and 0.2 Hz), resulting in nine experimental conditions. Each condition lasted 2 min and was performed four times in succession. Target sizes and movement frequencies were presented in random order. To estimate the impedance of the arm, six biphasic

torque pulse perturbations were applied by the motor during each 2-min trial. Four perturbation types were used (Fig. 2), and each was applied six times. The 24 perturbations in question were randomly distributed over the four 2-min trials. Trials were divided into sections of 20 s each, during which one perturbation was applied randomly in time, with the restriction that perturbations had to be ≥ 5 s apart. As seen in Fig. 2, all perturbations occurred in the zero crossing of the sine wave, i.e., at an elbow angle of 90° . Perturbations were biphasic and had a total duration of 140 ms.

Because we were interested in the physical state of the elbow joint before the perturbation, perturbations had a short duration (140 ms), leaving the participant insufficient time to voluntarily react to the perturbation, whereas the analysis was performed over a short time

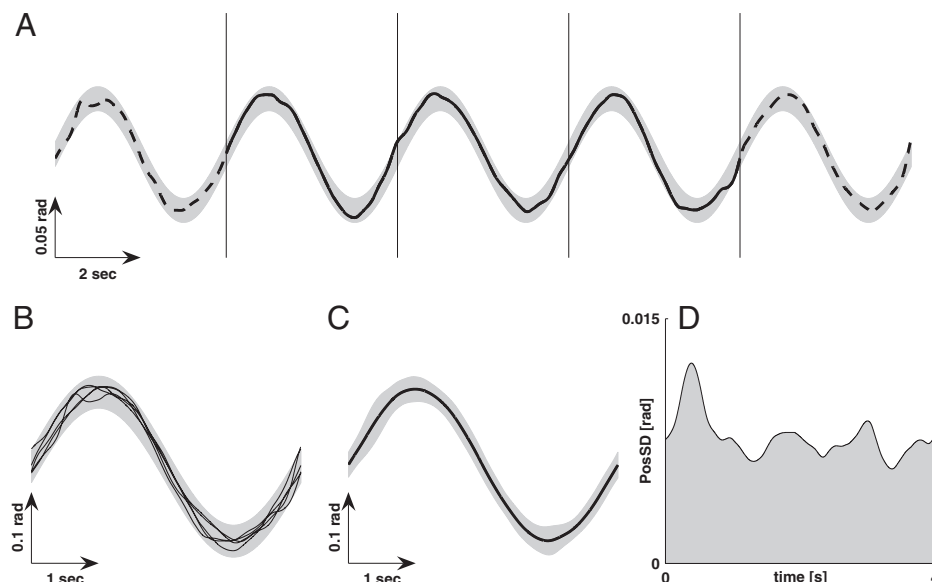


FIG. 3. Tracking variability. *A*: section of an experimental time series of elbow angle (black line) and target area (gray area). Vertical lines, boundaries of cycles. *B*: superposition of cycles (black lines) and target area (gray area). *C*: mean angle (black line) and 95% CI (gray area) over cycles. *D*: positional SD over movement cycles. Motor output variability was expressed as Ave-PosSD and calculated by taking the mean of the time series in *D*.

interval (170 ms), such that the inclusion of voluntary responses in the analysis was minimized. Furthermore, subjects were instructed to move naturally without trying to anticipate the perturbations and not to intervene voluntarily in response to the perturbations. Before the central part of the experiment, the same perturbations were applied to the relaxed arm to estimate the combined inertia of forearm and manipulandum.

Analyses

MOTOR OUTPUT VARIABILITY. The four angular position time series of each condition were rearranged into a matrix of cycles (Fig. 3). The variability of the unperturbed cycles was assessed by calculating the SD as a function of time

$$\text{PosSD}(t) = \sqrt{\frac{1}{n} \sum_{j=1}^{j=n} [\varphi_j(t) - \bar{\varphi}(t)]^2} \quad (1)$$

where n is the number of unperturbed cycles included in the analysis and t represents time within a cycle. The number of available unperturbed cycles differed for the three movement frequencies ($n = 96, 66$, and 48 for $f = 0.33, 0.25$, and 0.2 Hz, respectively). To avoid spurious decrease in PosSD because of the larger number of unperturbed cycles for the higher movement frequency, 48 unperturbed cycles were randomly drawn from the 0.25- and 0.33-Hz conditions. Subsequently, the time-averaged value of PosSD was calculated (AvePosSD). The percentage of samples that fell outside the target boundaries was determined to assess the degree to which subjects fulfilled the accuracy demands.

ESTIMATION OF ELBOW IMPEDANCE. To estimate the dynamics of the elbow joint in response to the mechanical perturbation, a second-order linear model with stiffness K , damping B , and inertia I (denoted as the K - B - I model) was fitted to the kinematic responses. The kinematic changes caused by the perturbation were quantified by subtracting the average movement cycle angular position $[\bar{\varphi}(t)]$ from the angular positions in the perturbed cycles $[\varphi_{\text{pert}}(t)]$, corrected for their distance at perturbation onset

$$\Delta\varphi_{\text{pert}} = [\varphi_{\text{pert}}(t) - \varphi_{\text{pert}}(t_0)] - [\bar{\varphi}(t) - \bar{\varphi}(t_0)] \quad (2)$$

The external moment generated in the perturbed cycles was measured directly by means of a strain gauge. During the unperturbed cycles, a small external moment was sensed by the strain gauge. The average external moment across unperturbed cycles $[\bar{M}(t)]$ was subtracted from the measured external perturbation moment $[M_{\text{pert}}(t)]$ and corrected such that its value was zero at perturbation onset

$$\Delta M_{\text{pert}} = [M_{\text{pert}}(t) - M_{\text{pert}}(t_0)] - [\bar{M}(t) - \bar{M}(t_0)] \quad (3)$$

The parameters of the K - B - I model were estimated using a combined optimization and simulation routine (Selen et al. 2006). In the forward simulation step, the kinematics (φ_{sim}) were simulated by imposing the measured external perturbation moment (ΔM_{pert}) to the K - B - I model. The inertia was determined from the perturbations to the relaxed arm, independently of the experimental manipulations. In the subsequent nine optimizations, estimates of K and B were obtained for the different experimental conditions. After the optimization, the variance accounted for (VAF) was calculated

$$\text{VAF} = 1 - \frac{[\Delta\varphi_{\text{pert}}(t) - \varphi_{\text{sim}}(t)] \cdot [\Delta\varphi_{\text{pert}}(t) - \varphi_{\text{sim}}(t)]^T}{[\Delta\varphi_{\text{pert}}(t)] \cdot [\Delta\varphi_{\text{pert}}(t)]^T} \quad (4)$$

CHARACTERIZATION OF SUBMOVEMENTS. Tracking movements are characterized by submovements that appear as oscillations in the velocity profile. Submovement characteristics were studied in both the frequency and time domain. The main frequency of the submove-

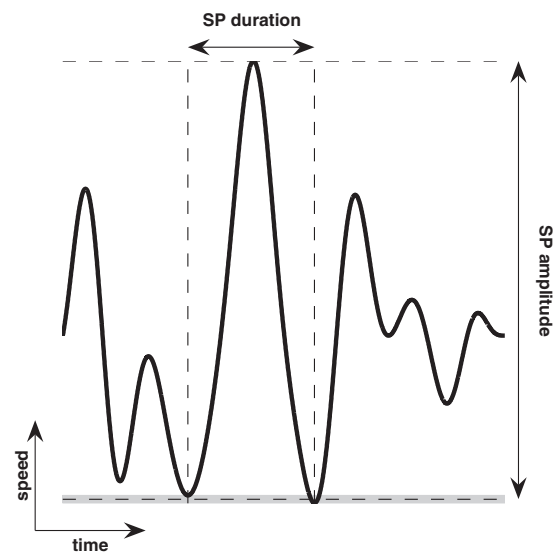


FIG. 4. Section of the speed profile, showing the speed pulses (SPs). Amplitude (SP amplitude) and duration (SP duration) of a single SP are indicated.

ments was identified as the second peak in the power spectrum (the 1st peak being the target movement frequency). To this aim, power spectra were calculated using Welch's averaged periodogram method. Each time series was divided into 50% overlapping sections of 2^{14} datapoints with a Hamming window, resulting in an average spectrum with a frequency resolution of 0.06 Hz.

Sophisticated submovement extraction algorithms have been proposed for the time domain (Rohrer and Hogan 2006), but most of them are only applicable to goal-directed movements with a small number of submovements. To examine the properties of the oscillatory behavior during tracking, we adopted the speed pulse (SP) analysis from Roitman et al. (2004) and Pasalar et al. (2005). Time series of angular position were low-pass filtered using a fifth-order Butterworth filter with a cut-off frequency of 6 Hz. This relatively low frequency was chosen to avoid spurious detection of submovements. Higher frequencies, such as the 12 Hz used by Roitman et al. (2004), shifted the mean and median SP duration to lower values that did not correspond to the main frequency as deduced from the power spectra.

Because we were interested in the movement in the target area independent of the movement of the target area itself, the motion of the target was subtracted¹

$$\varphi_{\text{rel}}(t) = \varphi(t) - A \sin(2\pi t/T) \quad (5)$$

Subsequently, the numerical derivative was calculated to obtain angular velocity time profiles. The duration of a single SP (SP duration) was defined as the time between two successive local minima in the velocity profile. The amplitude of a SP (SP amplitude) was defined as the difference between a local maximum in the velocity profile and the average value of the two nearest minima (Fig. 4). The linear regression between SP duration and SP amplitude provided an intercept and a slope. The latter was interpreted as error correction gain and will be referred to as SP gain in the remainder of this article.

Statistics

Both in the text and in the figures, the data will be presented as means and SD. Effects of target size and movement frequency on AvePosSD, SP duration, SP amplitude, and SP gain were analyzed using two-way repeated-measures ANOVAs (3 target sizes \times 3

¹ Note that, for both the impedance and SP analysis, the use of $A \sin(2\pi t/T)$ or $\bar{\varphi}(t)$ yields the same results.

movement frequencies). The effects of the experimental manipulations on the impedance estimates were examined by performing three-way (4 perturbation types \times 3 target sizes \times 3 movement frequencies) (M)ANOVAs on K and B separately and together. If the ANOVA revealed significant changes ($P < 0.05$), post hoc tests with Bonferroni correction were performed to identify differences. The effect size was quantified by partial η^2 (η_p^2). All statistical tests were performed using SPSS 11.5.

RESULTS

Accuracy manipulation

Figure 3 presents a typical example of movement variability for one subject in a single experimental condition. Movement variability was expressed as AvePosSD, which is the mean over time of the signal in Fig. 3D. Figure 5 shows that movement variability decreased with smaller targets ($F_{(2,14)} = 72.836$, $P < 0.000$, $\eta_p^2 = 0.91$) and lower movement frequencies ($F_{(2,14)} = 44.434$, $P < 0.000$, $\eta_p^2 = 0.86$), indicating that the experimental manipulation indeed induced an accuracy increment. However, a substantial number of samples fell outside the target boundaries and this number increased with smaller targets ($F_{(2,14)} = 204.762$, $P < 0.000$, $\eta_p^2 = 0.97$) and higher movement frequencies ($F_{(2,14)} = 37.120$, $P < 0.000$, $\eta_p^2 = 0.84$). Especially for the small target, the percentage of samples outside the target boundaries was large. This is reflected in the observation that AvePosSD did not differ significantly between the small and medium target.

Impedance modulation

The dynamics of the elbow joint was quantified by fitting a K - B - I model to the experimental data. The inertia was determined independently of the experimental manipulations and ranged from 0.0454 to 0.0729 Nms²/rad across subjects. The estimates of I were robust as indicated by the high VAFs (>0.99). Given the inertia, estimates of stiffness and damping

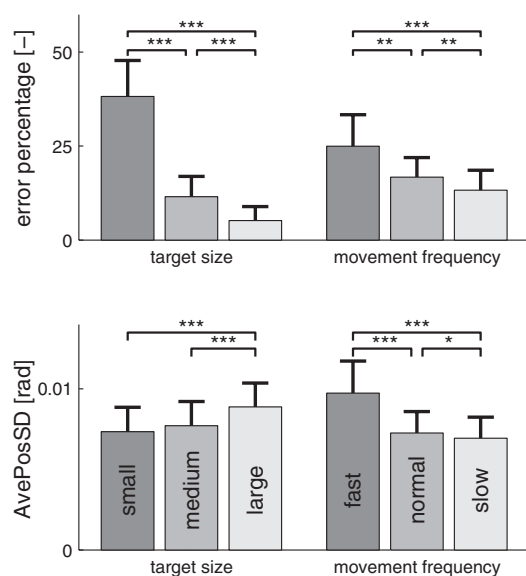


FIG. 5. Mean and SD over 8 subjects of the cycle ensemble kinematic variability [SD(t)] averaged over time (AvePosSD) and the percentage of samples outside the target boundaries (error percentage) for 3 target sizes (0.0135, 0.0270, and 0.0405 rad) and 3 movement frequencies (0.33, 0.25, and 0.2 Hz). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

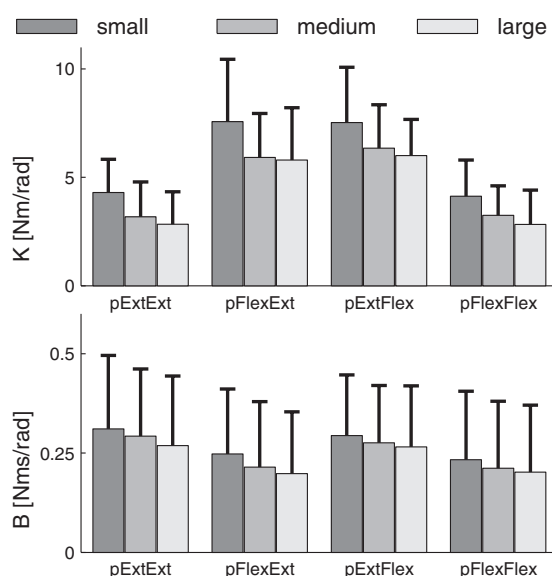


FIG. 6. Mean and SD of stiffness (K) and damping (B) over 7 subjects for 3 target sizes (0.0135, 0.0270, and 0.0405 rad) and 4 perturbation types. Data were averaged over movement frequencies.

were calculated for all experimental conditions. Again the VAFs were high (mean, 0.9935; range, 0.9527–0.9995), indicating that the K - B - I model accurately described the dynamics of the elbow. Bootstrapping the experimental data (Efron and Tibshirani 1993) revealed a coefficient of variation [(SD/mean) \times 100%] of the estimates of K and B of $<10\%$. Figure 6 indicates that both K and B decreased with increasing target size for all four perturbation types. Repeated-measures MANOVA revealed significant effects of both target size and perturbation type on K and B . Movement frequency did not influence K and B . Because stiffness and damping are not necessarily a measure of the same process, repeated-measures ANOVAs were also performed for K and B separately. The results of both analyses were similar. Table 1 presents the results of all statistical tests including all two-way interactions and η_p^2 as a measure of effect size.

Submovement gain modulation

Submovement characteristics were studied by calculating the duration and amplitude of speed pulses (Pasalar et al. 2005; Roitman et al. 2004). SP gain was defined as the slope of the regression between SP duration and SP amplitude. SP gain accounted for $>70\%$ [$R^2 = 0.71 \pm 0.07$ (SD)] of the observed variance in the data points. Figure 7 presents scatter plots of all combinations of SP duration and SP amplitude for the nine experimental conditions for a typical subject. The linear regression line is superimposed. Repeated-measures ANOVAs (Table 2; Fig. 8) revealed that SP gain declined with decreasing movement frequency and increasing target size. The average duration of a SP was independent of movement frequency and target size. SP amplitude decreased with decreasing movement frequency and increasing target size and accounted for the increase in SP gain. Figure 9 presents the average power spectral densities for all experimental conditions. The sharp peak corresponds to the movement frequency, whereas the broad peak corresponds to the frequencies of the speed pulses. The SP peak (F_{main}) did not shift with target size ($F_{(2,14)} =$

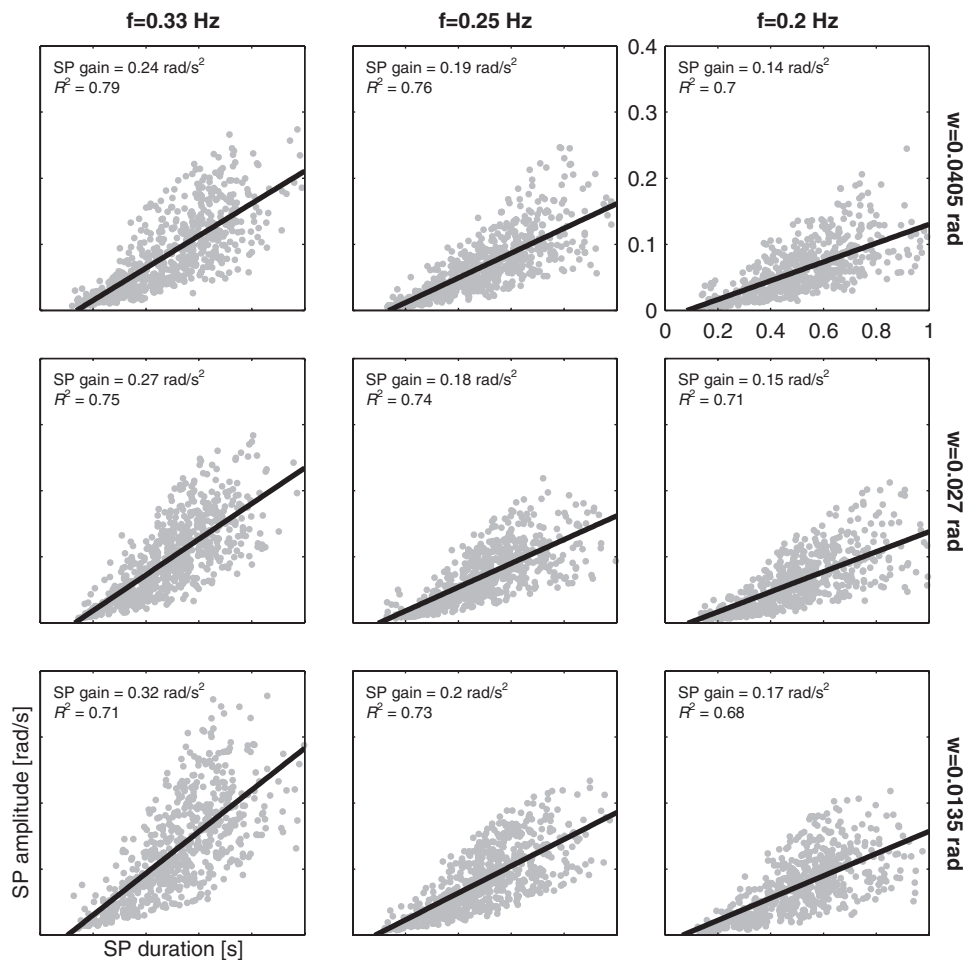


FIG. 7. SP gain for a single subject for 3 movement frequencies (columns) and 3 target sizes (rows). SP gain is the regression slope of SP duration vs. SP amplitude.

2.692, $P = 0.101$, $\eta_p^2 = 0.31$) or movement frequency ($F_{(2,14)} = 0.911$, $P = 0.424$, $\eta_p^2 = 0.13$).

DISCUSSION

The first purpose of this study was to examine the effects of both target size and movement frequency on the mechanical impedance of the elbow during single-joint target tracking. It was found that the mechanical impedance of the elbow, quantified by K and B , increased with smaller targets but was unaffected by target frequency. The second purpose was to study adaptations in submovements with variations in target size and movement frequency. SP gain increased with increasing task difficulty, i.e., with smaller targets and at higher movement frequencies. In the following sections, the results for impedance modulation and SP gain modulation will be discussed in turn.

Mechanical impedance

MODULATION WITH TARGET SIZE AND MOVEMENT FREQUENCY. The fact that K and B increased with smaller targets is consistent with the hypothesis, introduced by Van Galen and colleagues (Van Galen and De Jong 1995; Van Galen and Schomaker 1992), that increased mechanical impedance acts as a filter of intrinsically noisy neuromuscular signals. Although

this hypothesis found support in EMG studies (Gribble et al. 2003; Laursen et al. 1998; Osu et al. 2004; Sandfeld and Jensen 2005; Seidler-Dobrin et al. 1998; Van Roon et al. 2005; Visser et al. 2004), supporting mechanical evidence has been few and far between. In a previous study, we showed that the mechanical impedance increases with increasing accuracy demands when approaching the target in goal-directed aiming (Selen et al. 2006). In this study, this finding was generalized to a situation in which accuracy demand and movement velocity were prescribed continuously by the sinusoidal movement of the target.

Besides an effect of target size, we expected the impedance to increase with increasing frequency (i.e., peak velocity). Our reasoning in this regard was as follows. Higher movement frequencies require larger propelling forces, which coincide with greater neuromuscular noise (Jones et al. 2002; Schmidt et al. 1979), necessitating increased impedance to attain the required accuracy. Moreover, even without impedance modulation, movement frequency by itself increases impedance as a result of muscle mechanics. As a case in point, Milner (1993) measured the angular displacement produced by a torque pulse (5 Nm and 50 ms) and reported a decreasing displacement when movement velocity increased from 2 to 4 rad/s. He argued that higher movement velocities are accompanied by higher propelling forces, requiring more attached parallel cross-bridges, coinciding with higher muscle stiffness and

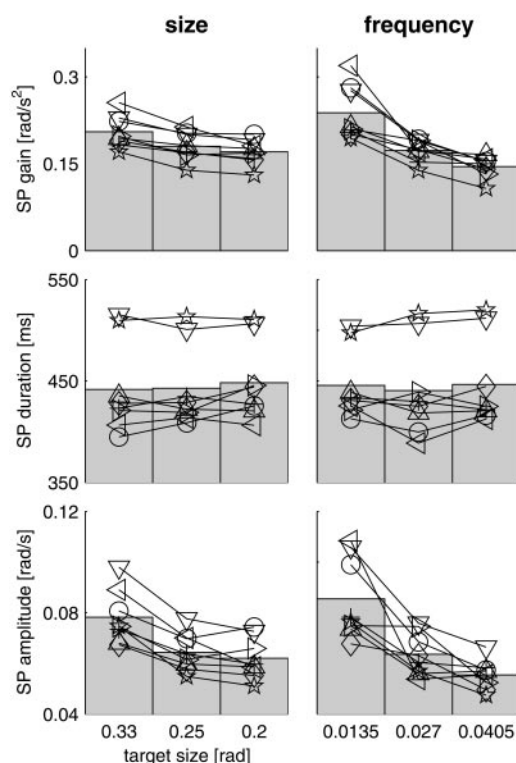


FIG. 8. Group mean values for SP gain, SP duration, and SP amplitude for movement frequency and target size. Individual means for the subjects are superimposed. Repeated-measures ANOVAs indicated significant effects for SP amplitude and SP gain.

consequently higher joint stiffness. Unexpectedly, we found that, across the frequencies tested, the impedance of the elbow remained constant. Apparently, the preceding arguments did not hold at the low movement frequencies employed. Peak velocity of the target ranged from 0.1 to 0.2 rad/s, resulting in discontinuous control of movement velocity. As a consequence, the propelling forces for the resulting submovements were relatively low and did not contribute significantly to joint stiffness and force variability.

A further consideration is that lower movement frequencies allow for more visually guided feedback corrections per movement cycle and therefore would require less feedforward impedance control given the prevailing accuracy constraints. We observed that SP duration remained constant with movement frequency, resulting in ~33 and 66% more corrective movements per movement cycle for the 0.25- and 0.2-Hz movements compared with the 0.33-Hz movement. Because increased impedance is energetically costly, it was expected that subjects would decrease mechanical impedance whenever possible. However, the achieved accuracy levels were lower than the levels demanded by the target size (Fig. 5). Apparently all available sources for variability reduction were deployed, and none was lowered with decreasing movement frequency.

Joint stiffening has been associated with learning novel tasks (Bernstein 1967). When confronted with a new task, degrees of freedom are frozen by stiffening joints and over the course of learning the stiffness decreases, gradually releasing degrees of freedom. However, this concept pertains to learning the dynamics of a novel multijoint movement (Franklin et al. 2003). The single-joint task studied here precludes freezing degrees of

freedom. Furthermore, the dynamics of the task did not change between the different target sizes.

PARAMETER VALUES. The *average* stiffness values reported in this study are in the same range as those found for the elbow in goal-directed aiming (Bennett 1993; Kalveram et al. 2005; Selen et al. 2006). Bennett et al. (1992) estimated the time-varying stiffness of the elbow joint during paced reciprocal aiming in the horizontal plane. At peak velocity, the instant of perturbation initiation in this study, their stiffness estimates (3 Nm/rad) were lower than the average stiffness in this study (5–6 Nm/rad). Most likely this is because of continuous control of impedance in response to accuracy constraints in this study, whereas in the study of Bennett et al. (1992), stiffness was probably only controlled when approaching the targets (Osu et al. 2004; Selen et al. 2006).

As expected, stiffness modulation with increasing target size was much stronger in the present target tracking study than observed for goal-directed movements (Selen et al. 2006). Tracking movements were more consistent and probably involved continuous impedance control to attain the required accuracy. Although the overall pattern of impedance modulation with accuracy and frequency demands was robust (Fig. 6), the stiffness values differed significantly across the four perturbation types. The highest stiffness values were found when the onset direction of the perturbation opposed the movement direction. In all likelihood, this perturbation type dependency was caused by the interaction of motor and elbow joint dynamics in combination with the nonlinearity of the system (Kay et al. 1991; Kearney and Hunter 1990; Kirsch et al. 1994).

Quantification of the mechanical impedance of the musculo-skeletal system has a long history (see Kearney and Hunter 1990). The mechanical impedance of a system is best described by its transfer function, which can only be estimated using continuous perturbations. However, such perturbations interact with the natural behavior of the motor control system (Kirsch et al. 1994). Transient perturbations, as used in this study, provide information about the state of the system just before the perturbation. Making a priori assumptions about the system under study is inevitable when quantifying impedance. In this study, the musculo-skeletal system was approximated with a second-order model. The elbow joint system is of much higher order, and one might therefore question the exactness of the obtained stiffness and damping estimates. However, we were interested in the modulation of stiffness and damping and not in their exact values.

The time window over which changes in stiffness and damping were observed suggests that both intrinsic muscle properties and reflex components contributed to impedance modulation. Even voluntary reactive activity may have occurred at the very end of the estimation window. However, we believe that the instruction to the subjects not to intervene, effectively suppressed voluntary responses. This is supported by the high consistency of the kinematic traces. Only after the estimation window of 170 ms did the traces start to disperse (Fig. 2).

Submovement characteristics

The second purpose of this study was to examine how submovement characteristics, such as SP duration, SP ampli-

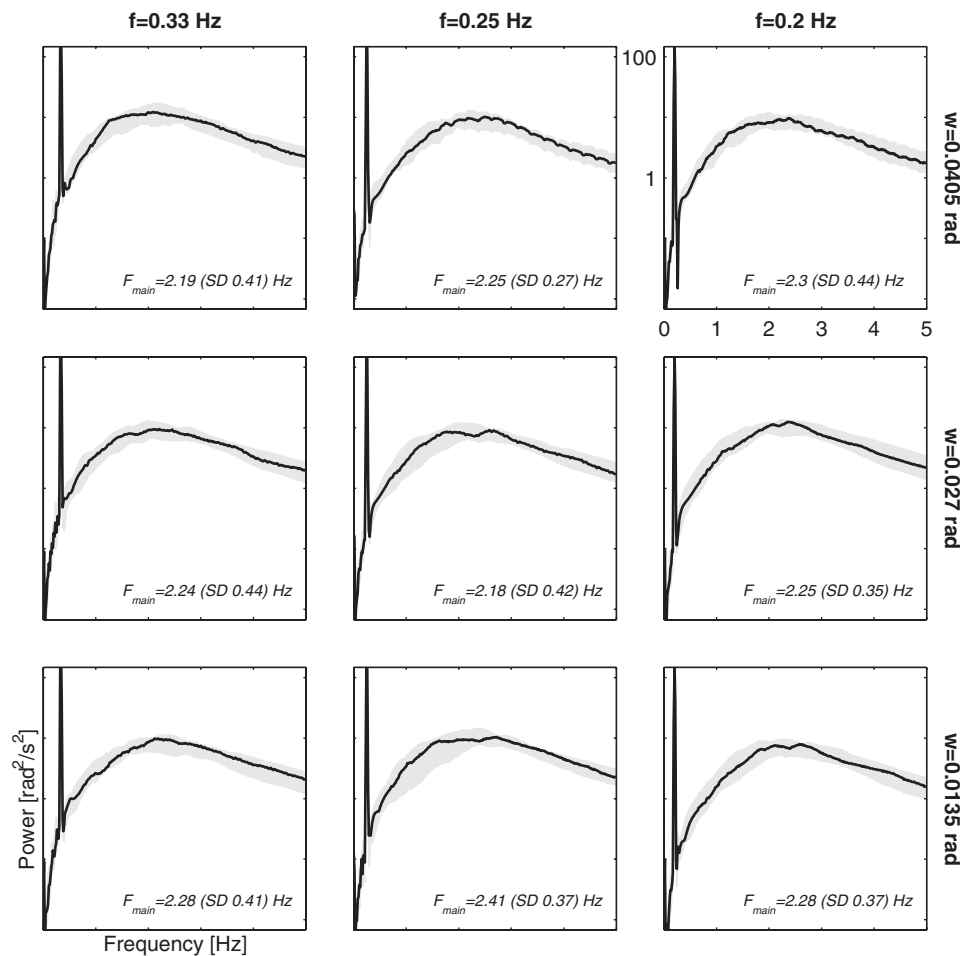


FIG. 9. Power spectra averaged over all subjects (black line) for 3 movement frequencies (columns) and 3 target sizes (rows). Gray area, 95% CI. Sharp peaks, movement frequencies; broad peaks, caused by SPs. F_{main} is the main frequency of the SPs.

tude, and SP gain, relate to task constraints (i.e., movement frequency and target size). For movement frequency variations, we had explicit hypotheses derived from the literature, but for the target size manipulation, our study was more explorative.

For increasing movement frequency, we observed an increase of both SP amplitude and SP gain and no effect for SP duration, consistent with previous results for sinusoidal tracking in monkeys (Miall et al. 1986) and constant velocity circular drawing of monkeys (Roitman et al. 2004) and humans (Pasalar et al. 2005). We share the interpretation of Pasalar et al. (2005) that increases in SP gain are a consequence of the greater tracking errors generated at faster speeds. During a fixed time interval, faster targets travel further, necessitating larger corrections resulting in larger SP amplitude and SP gain. The constancy of SP duration either suggests that more frequent corrections are impossible or inconvenient.

Changes in submovement characteristics in relation to target size have not been studied before. For decreasing target size, we observed increases in SP amplitude and SP gain, whereas SP duration was unaffected by target size. These results indicate that submovements are organized differently in tracking movements compared with goal-directed movements. As we highlighted in the introduction, goal-directed movements, unlike tracking movements, allow for more subtle, i.e., more frequent and smaller, submovements when aiming for smaller targets.

Pasalar et al. (2005) examined the effects of external force field magnitude on the regulation of submovements in circular drawing. SP gain and SP amplitude increased with increasing force field magnitude, whereas SP duration decreased. Pasalar et al. (2005) argued that SP gain was tuned in response to tracking errors by showing that tracking error increased with faster speeds as well as with higher force field magnitudes. The same argument might hold for the varying target sizes in this experiment. If we assume that tracking errors are defined in units of target size, the same absolute error will generate a larger correction, reflected in SP gain, for the smaller target.

Are impedance modulation and changes in the organization of submovements as a function of variations in task conditions related? Or, put more specifically, could the observed changes in the submovements be caused by changes in the natural frequency of the forearm because of stiffness changes? The data suggest that this was not the case. Given the inertia and stiffness estimates obtained, the natural frequency of the forearm would be $\sim 1.5 \pm 0.38$ Hz, which is lower than the identified frequency of the submovements. Furthermore, the natural frequency varied as a function of the experimental conditions, whereas submovement duration seemed constant across conditions. Both observations indicate that impedance modulation and SP gain changes represent independent and additive accuracy control mechanisms. The frequency content

of the speed profiles of ~ 2 Hz, as deduced from the frequency and time series analyses, suggests that the speed pulses are driven by visual feedback.

Generalization to multijoint movement

Single-joint movements occur rarely in daily life. It is therefore important to study whether the findings of this study on single-joint movements can be generalized to more natural, multijoint movements. There exists only indirect evidence for impedance modulation in response to accuracy constraints in multijoint movements. Muscular coactivation increases in response to higher accuracy constraints in pointing movements (Gribble et al. 2003; Laursen et al. 1998). Studies on multijoint movement do show that humans are able to adapt endpoint stiffness to the instability of the task and that this increased stiffness reduces trajectory variability (Burdet et al. 2001). The question is whether multijoint impedance also changes in response to accuracy demands. An indication to this effect can be gleaned from the work by Perreault (2005), showing that subjects orient their endpoint stiffness (largely dependent on body configuration) in line with the accuracy constraint.

The effects of movement speed on the organization of submovements was previously studied in multijoint movement (Pasalar et al. 2005; Roitman et al. 2004). The results were similar to our results in the single-joint case. To our knowledge, however, the effects of accuracy constraints on the organization of submovements have not been studied before.

In summary, this study underscores the importance of impedance modulation in controlling movement accuracy. It supports the claim of Van Galen and De Jong (1995), and Van Galen and Schomaker (1992) and the experimental findings of Burdet et al. (2001) and Selen et al. (2006) that greater impedance enhances movement accuracy. Furthermore, this study provides new evidence that intermittently controlled submovements are natural components of motor behavior and that their characteristics are modulated in response to task constraints, such as accuracy demands. The data suggest that impedance modulation and SP gain modulation contribute additively, i.e., independently, to the accuracy of target tracking.

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